Clutch Size and Laying Date in the Kestrel Falco Tinnunculus

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CLUTCH SIZE AND LAYING DATE IN THE KESTREL *FALCO TINNUNCULUS:* EFFECT OF SUPPLEMENTARY FOOD

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Clutch size and laying date in avian breeding were originally proposed by Lack (1947, 1968) to have evolved such that birds conforming to the population average in the long run contribute most offspring to the next generation. This view had to be modified when the most productive clutch turned out to be larger than average and to be laid earlier than average (Perrins 1965, 1970, Cavé 1968). These findings prompted the hypothesis that food, differentially available to different females in the

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population, restricts the early date and size of the clutch, such that only a minority can achieve the optimal strategy (Perrins 1965, Lack 1968). Attempts to test the hypothesis experimentally have made use of supplementary food presented during the pre-laying period in three species of bird. Food supplements caused a *c.* six-day advance in laying date of the Great Tit *Parus major* (Kjällander 1974), a five-day advance in Carrion Crows *Corvus corone* (Yom-Tov 1974) and had no significant influence on laying date in Magpies *Pica pica* (Högstedt 1980). A slight effect on clutch size was observed only in the Magpie study, in one of two experimental years. In similar experiments in Kestrels, a species with large annual variations in clutch size and laying date, associated with variations in vole abundance (Cavé 1968), we have obtained evidence for a simultaneous influence of food on both parameters.

The experiments done in connection with a study on the role of the energetics of behaviour in Kestrel survival (Rijnsdorp, Daan & Dijkstra 1981), were carried out in a recent land reclamation area the Lauwersmeer. This area is populated by *c.* 30 pairs of Kestrels breeding in nest boxes. Some boxes were supplied with dead white laboratory mice prior to laying. This was done every two days, starting on 28 January 1978, 10 March 1979 and 4 March 1980, and lasting until the female Kestrel had started incubation. Daily rations fed to a pair varied between 100 and 120 g, corresponding to about twice the daily existence metabolism of Kestrels in captivity (Kirkwood 1979). Evidence that the Kestrels fed on the mice was obtained by direct observation and by collection of white pellets regurgitated. Table 1 presents laying dates and clutch sizes of those pairs which took the additional food from before 12 March onwards, as well as for control pairs in the area. Three pairs took the food only after 12 April (one in 1979 and two in 1980) and were excluded from the control group.

As in the study by Cavé (1968), clutch size and laying date varied considerably with vole abundance. In peak vole years (1977, 1980) clutches were laid *c.* 14 days earlier and contained on average about one more egg than in a low year (1978). The breeding season of 1979 was characterized by medium vole abundance and by a very late spring following a severe winter during which the entire Kestrel population had left the area. In this year only two pairs returned in time to receive the food supplement. In 1980 the data were incomplete due to human interference with some of our experimental pairs. The interpretation of the 1980 data is further complicated by the

TABLE 1

Clutch size (eggs) and laying date of the first egg of Kestrels in the Lauwersmeer area. Three pairs starting to take the additional food after 12 March and two bigamous females in 1980 are excluded. Means ± *s.d.* (n). *Data for 1978 and 1979 are pooled in three groups: group A, experimental pairs; group B, control pairs in nest boxes occupied before 12 March; group C, control pairs in nest boxes not occupied before 12 March*

	Vole abundance	Control pairs		Experimental pairs	
		Laying date	Clutch	Laying date	Clutch
1977	++	24 April ±14(19)	5·4±0·9(19)	—	—
1978	0	8 May ±15(17)	4·6±0·9(17)	6 April ±5 (4)	5·7±0·5(4)
1979	+	10 May ±12(13)	4·5±0·9(13)	17 April (2)	5 (1)
1980	++	25 April ±12(18)	5·6±0·7(17)	23 April (3)	6 (2)
1978/79:		Group B		Group A	
		3 May ±15(11)	4·6±1·2(11)	10 April ±7 (6)	5·6±0·5(5)
		Group C			
		14 May ±11(19)	4·5±0·7(19)		

fact that the experimental pairs were in a restricted area, geographically separated from the controls.

In 1978 experimental pairs laid *c.* 30 days in advance of the controls, and had average clutches more than one egg larger. The two experimental pairs in 1979 laid well ahead of the controls (23 days), the two in 1980 did no better than the controls. The long food treatment in the low vole year of 1978 induced in the four experimental pairs a performance close to that of the best pairs in peak vole years (1977 and 1980) in terms of clutch size and laying date (Fig. 1). This may be close to the absolute constraints posed by circannual rhythmicity and incubation capacity.

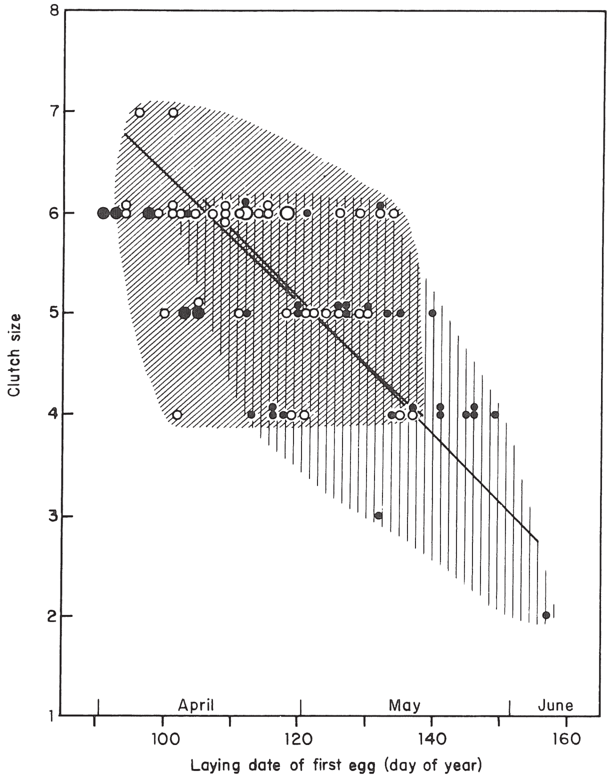

FIGURE 1. Dependence of Kestrel clutch size on laying date in years with abundant (○; 1977, 1980) and poor vole supply (●; 1978, 1979). Shaded areas encompass all data points of control birds. Lines are the long axes through the two clouds of data points, obtained by principal component analysis: rich years: $y = 12{\cdot}57 - 0{\cdot}062x$; poor years: $y = 13{\cdot}24 - 0{\cdot}067x$. Enlarged symbols indicate data for seven pairs receiving additional food starting between 1 February and 12 March.

The addition of food in 1978 and 1979 may not have been solely responsible for the differences between experimental and control pairs. Those birds which were not yet present in the area when the experiments started are only represented in the control group and not in the experimental group. These birds in particular may have had late and small clutches. To analyse the effects of food and early or late arrival in the area separately we distinguished between a group (B) of control pairs in nest boxes that were occupied already before 12 March (the latest date of occupation in the experimental group A) and a group (C) of nests occupied after that date. Mean laying date was 23 days earlier in group A than in group B (Wilcoxon-test $P < 0{\cdot}001$), and 11 days earlier in group B than in group C ($P < 0{\cdot}05$). In clutch sizes, significance of the differences was marginal, ($P < 0{\cdot}1$) between group A and B and absent ($P > 0{\cdot}1$) between B and C.

We take the data to imply that at least in years with vole scarcity, food availability restricts both clutch size and laying date in the Kestrel. They confirm Cavé's conclusion, which was based on correlations both among years and among parts of his study area. In years with abundant natural food, the two parameters may be restricted in some other way, although this awaits further experimentation.

Clutch size and laying date are negatively correlated with each other in the Kestrel as in many other species (Fig. 1). The simultaneous response of these parameters to rich food supplies, both natural and experimental, is in accord with this correlation. We do not know if the larger clutch size due to extra food is a mere consequence of earlier laying or, alternatively, if the two parameters are independently affected by food. The axes through the point clouds of the distribution, obtained by principal component analysis are virtually identical for rich and poor vole years (Fig. 1). Although this might suggest that the birds' circannual machinery allows them only to shift diagonally along this one axis, other interpretations are possible. It is not excluded that clutch size can be affected by food intake independently of laying date. It was recently suggested that the optimal clutch size is generally large for an early laying female and small for a late female (Drent & Daan 1980). While such a strategy, based on the chances of survival for eggs laid at different times of year, may be usually adopted, it is not excluded that a late female faced with a sudden rich food source would adjust her clutch size in spite of the advanced breeding season. Experiments with supplementary feeding late in the year will be a next step to unravel the significance of the response to food.

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